CHROMOSOME CYTOLOGY OF *HESSEA*, *STRUMARIA*, AND *CARPOLYZA* (AMARYLLIDACEAE)

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ABSTRACT

A diploid number of $2n = 20$ is reported in *Carpolyza*, in the four species of *Strumaria*, and four of the five species of *Hessea* studied. One species, *Hessea zeyheri*, has $2n = 22$. Similarity of karyotypes in all the species with $2n = 20$ appears to indicate a close relationship between them. *Hessea zeyheri* with $2n = 22$ may be a link between the $x = 10$ group and the remainder of the tribe Amaryllideae in which $x = 11$ is basic. The possible systematic significance of the difference in base number in *Hessea zeyheri* is explored and a reevaluation of generic limits is suggested.

The genera of *Hessea*, *Strumaria*, and *Carpolyza* comprise what seems a natural alliance in the Amaryllidaceae. Their overall geographical range is limited to the drier regions of southern Africa, including the winter rainfall region of the Cape Province. The three genera share the following characteristics: a bulb with fibrous tunics of the *Crinum* type; small, white to pink, ± actinomorphic flowers, perianth tube short or lacking; distinctive soft fleshy seeds, such as are found in the tribe Amaryllideae[2], which break through the poorly developed capsule even before they mature. *Hessea* and *Strumaria*, as presently circumscribed, each comprise approximately ten species while *Carpolyza* is monotypic. *Carpolyza* is very distinct, but generic differences between *Hessea* and *Strumaria* are not clear and appear in need of reevaluation.

In spite of the contrary opinions of systematists such as Hutchinson (1959) and the earlier workers, Pax & Hoffmann (1930), and Herbert (1837), I am convinced that *Hessea*, *Strumaria*, and *Carpolyza* are closely related, and that their affinities lie with the tribe Amaryllideae, which includes amongst others, *Amaryllis*, *Crinum*, and *Nerine*. The characters shared are such fundamental features as the peculiar fibrous bulb tunics and fleshy, soft seeds. This relationship has only recently been recognized by Traub (1965), who places all three genera in the Amaryllideae (which he treats as Crineae).

The present cytological study is an attempt to obtain more information on the relationships of the three genera to one another and to the tribe Amaryllideae. Until now the cytology of only two species was known (Wilsenach, 1965) and, as is now clear, neither record is representative of the group as a whole. The

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[2] I am compelled to accept the opinions and conclusions of Sealy (1939), Dyer (1954) and Dandy & Fosberg (1954) regarding the identity of *Amaryllis belladona* L., the type of the Amaryllidaceae, i.e., applied to the S.W. Cape species. In contrast, Uphof (1938), Traub (1954, 1963), and Traub & Moldenke (1949) regard the species as a New World plant (= *Hippeastrum*). The arguments raised by Uphof, Traub, and Moldenke, correct up to a point, ignore the existence of a specimen of the Cape plant in the Cliffort Herbarium which almost certainly is the holotype. A detailed discussion of the opposing arguments need not be repeated, as the evidence has been fully presented elsewhere. In the terminology of Traub, Crineae is equivalent to the Amaryllideae as used here.

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present work comprises chromosomal data on ten species in all three genera, ± half of the species in the alliance. Species are all relatively rare and local, do not bloom regularly, and are thus very difficult to obtain. I hope eventually to collect further species for study but results at the present time merit publication, as there is no reason to believe further species will come to hand in the foreseeable future.

METHODS AND MATERIALS

Plants used in this study were all collected in the wild. Some had been in cultivation at the Kirstenbosch Botanical Gardens, Cape Town, South Africa, for a short time. Mitotic preparations only were made, root tips being collected from sprouting bulbs or from germinating seeds.

The same cytological technique as described earlier for the genus *Nerine* (Goldblatt, 1972) was employed, involving pretreatment in 0.05% colchicine, maceration in 10% HCl and squashing in lacto-propionic orcein.

CYTOLOGY

A basic chromosome number of $x = 10$ for the three genera seems indicated (Table 1) with $2n = 20$ found in all but one of the species studied (Figs. 1–2). The exception, *Hessea zeyheri*, is problematic; three populations were examined and a diploid number of $2n = 22$ seems most likely. While $2n = 22$ was the lowest number found, some plants in all three populations have $2n = 23$, 24, or even 25; $2n = 24$ was reported by Wilsenach (1965) for this species. The reason for proposing $2n = 22$ as the correct diploid number in *H. zeyheri* is not only that this was the lowest number encountered in the species, but where this number was exceeded, the extra chromosomes were quite small and appeared to lack centromeres. This makes it very likely that these are supernumeraries, and they are here regarded as B-chromosomes. Other workers have also encountered B-chromosomes in the Amaryllideae, notably Jones & Smith (1967) who recorded them in *Crinum*. Since $x = 11$ is almost certainly basic in the tribe, reports of $2n = 24$ in, for example, *Nerine* (e.g., Gouws, 1949) also probably indicate the presence of supernumerary chromosomes.

The only other previous count for the group, $2n = 22$ in *Strumaria truncata*, (Wilsenach, 1965) is not supported; two populations studied here had $2n = 20$, with karyotypes matching other species in the genus (Fig. 1B). In a third population individuals of *S. truncata* were found with $2n = 21$, the extra chromosome rather small and as in *H. zeyheri*, regarded as a B-chromosome. It seems likely that the karyotype described by Wilsenach consisted of $2n = 20 + 2B$, a suggestion supported by his illustration in which the 11th pair is much smaller than the others and almost telocentric.

As can be seen from the illustrations, the karyotypes of all four species of *Strumaria* and of three of the species of *Hessea*, *H. gemmata*, H. sp., and *H. chaplinii*, are all very similar (Figs. 1, 2A–C). This karyotype consists of a very long metacentric pair, four somewhat shorter ± submetacentric pairs, an acrocentric chromosome pair with a very large satellite much exceeding the shorter

TABLE 1. Chromosome number in *Strumaria*, *Hessea*, and *Carpolyza*. The following abbreviations are used: C.P. = Cape Province; S.W.A. = South West Africa.

Species	$2n$	Collection Data or Previous Count
Strumaria		
S. cf. *bidentata* Schinz.	20	S.W.A.; 15 km E of Witputs, *Tolken 3989* (BOL).
S. *rubella* Jacq.	20	C.P.; 5 km N of van Rhynsdorp, N.B.G. expedition 171/65 (NBG).
S. *truncata* Jacq.	20	C.P.; 30 km W of Bitterfontein, Namaqualand, *Hall s.n.* (NBG). SW of Wildeperdehoek Pass, Namaqualand, *Hiemstra 493* (NBG).
	20, 20 + 1B	C.P.; Near Kamieskroon, Namaqualand, *Goldblatt* (MO, NBG).
	22	(Wilsenach, 1965).
S. sp.	20	C.P.; Top of van Rhyns Pass, *Tolken 4003* (BOL).
Hessea		
H. *gemmata* (Ker) B. & H.	20	C.P.; Soetmelksrivier, W of Albertinia, *Lewis 5915* (NBG).
H. sp.	20	C.P.; Droerivier, van Rhynsdorp dist., *Tolken 3997* (BOL).
H. *chaplinii* Barker	20	C.P.; Paternoster, Saldanha dist., *Thomas s.n.* (NBG).
H. *tenella* (L.f.) Oberm.	20	C.P.; Rondebosch Common, Cape Peninsula.
H. *zeyheri* Baker	22, 23(22 + 1B), 24 (22 + 2B)	C.P.; Spektakelberg Pass, Namaqualand, *Goldblatt 2018* (MO, NBG).
	24(22 + 2B), 25(22 + 3B)	C.P.; E of Pakhuis Pass, *Goldblatt 1849* (MO, NBG).
	24(22 + 2B)	C.P.; Near Bullshoek, Olifants River Valley, *Goldblatt*, no voucher.[a]
	24	(Wilsenach, 1965).
Carpolyza		
C. *spiralis* Salisb.	20	C.P.; Imhofs Gift, Cape Peninsula, *Esterhuysen 32612* (BOL). Cogmans Kloof, Montagu, *Goldblatt 2102* (MO). Rivierson-end, *Goldblatt 2054* (MO).

[a] Determination provisional, flowers not seen.

chromosome arm, and four shorter pairs. Size distinctions are not always clear cut, and chromosomes do grade in size. Nevertheless, this description represents the situation fairly accurately.

Hessea tenella has a similar karyotype except that the satellite is in a different position, on the second longest pair which is acrocentric (Fig. 2D).

Carpolyza also has a slightly different karotype; here the longest pair is acrocentric in contrast with the usually metacentric long pair. In other respects, including the large satellite on a small chromosome pair, the karyotype conforms to the general condition. The chromosomes of this species seem slightly smaller than in others but not to any significant degree (Fig. 2F).

The cytology of *Hessea zeyheri*, with diploid counts ranging from $2n = 22$–25, is all the more remarkable in view of the almost uniform pattern in the remainder of the species studied. The karyotype comprises three large ± acrocentric pairs,

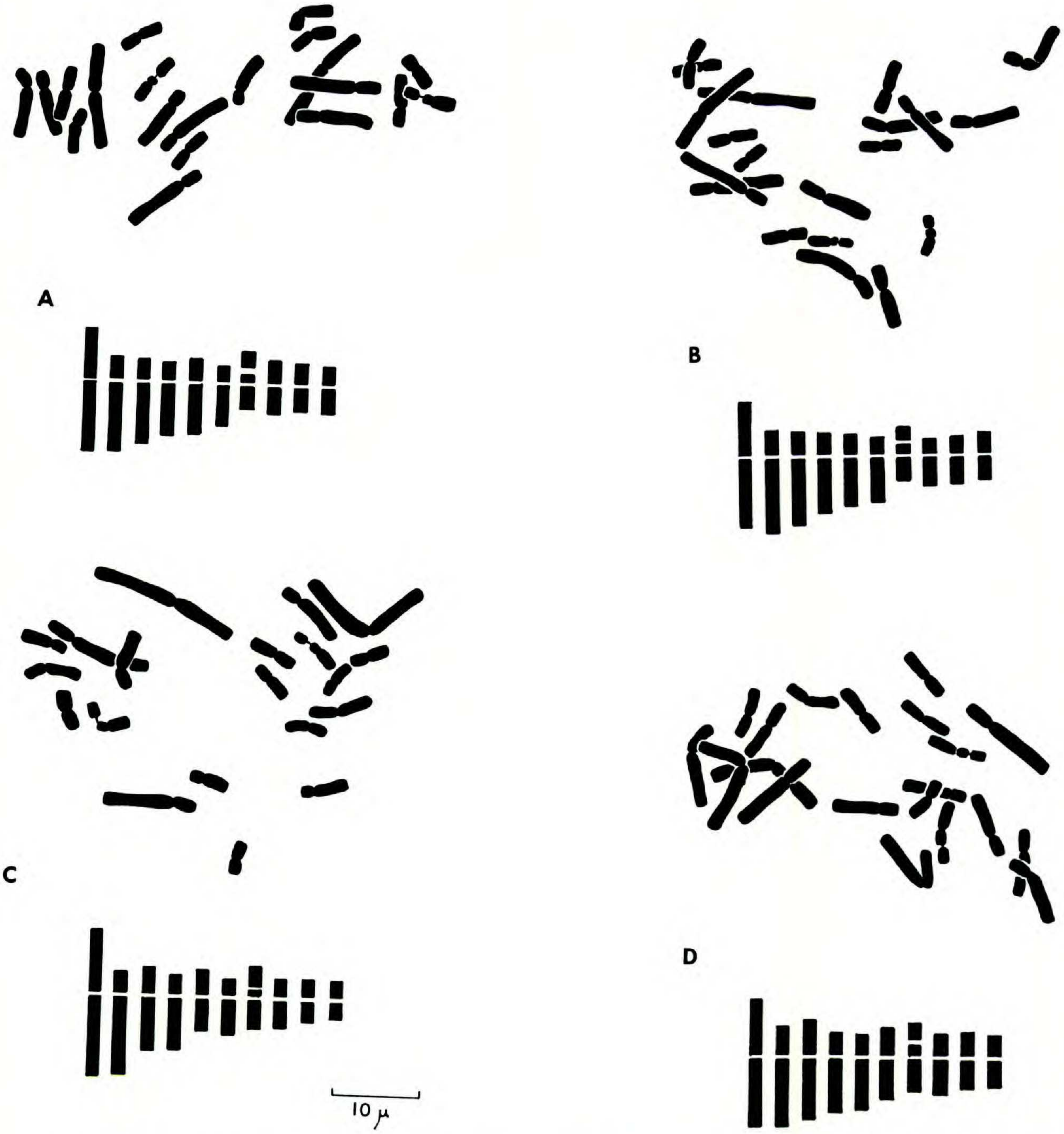

FIGURE 1. Mitotic metaphase and karyotypes in *Strumaria*.—A. *S. rubella*.—B. *S. truncata*.—C. *S.* sp.—D. *S.* cf. *bidentata*.

a fourth acrocentric pair with a very long satellite, and between 14 and 17 much smaller chromosomes mostly submetacentric but with telocentrics in cells with more than $2n = 22$. The basic number in this species is, as already suggested, probably $x = 11$, with a variable number of supernumerary, telocentric chromosomes occurring in many individuals.

The difference between the karyotype of this species and the more usual one in *Hessea* and *Strumaria*, apart from the supernumeraries, is that *H. zeyheri* has considerably more small chromosomes (Fig. 2E) while the other species have an extra two large chromosome pairs. The configuration of the chromosomes thus suggests the possible derivation of the more common $x = 10$ karyotype from the $x = 11$ condition in *Hessea zeyheri*, partly by Robertsonian translocation. Con-

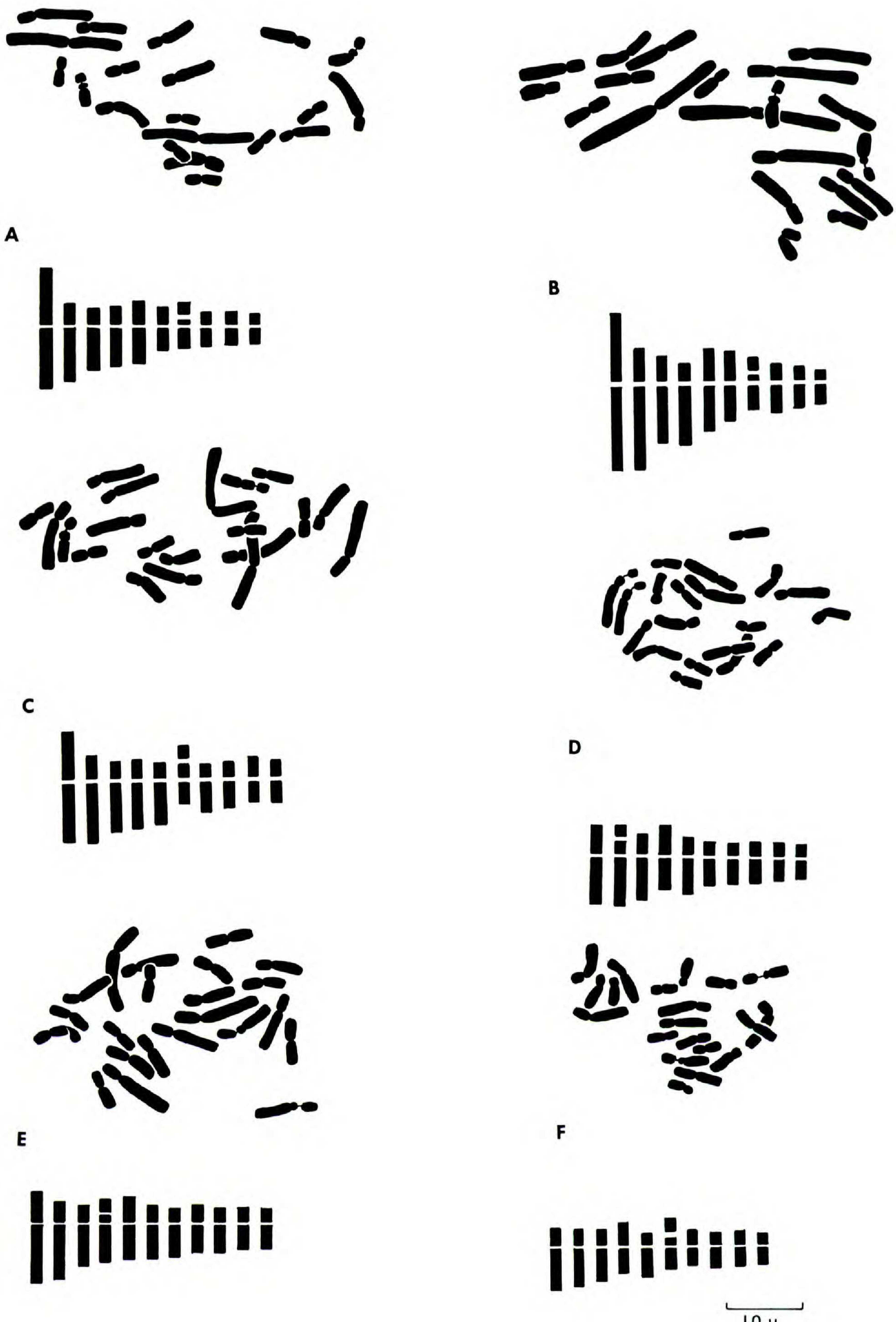

FIGURE 2. Mitotic metaphase in *Hessea* and *Carpolyza*.—A. *Hessea* sp.—B. *H. chaplinii*.—C. *H. gemmata*.—D. *H. tenella*.—E. *H. zeyheri*.—F. *Carpolyza spiralis*.

siderable chromosomal rearrangement is also indicated for the karyotype of *H. zeyheri* to approximate the condition in the other species examined. This suggestion assumes that reduction in number took place and there is some reason to believe that *H. zeyheri* is ancestral or primitive in the group, as discussed below.

DISCUSSION

All species of *Hessea, Strumaria*, and *Carpolyza* are small plants with small flowers, and it seems likely that they are reduced relatives of the large group of Amaryllideae that evolved locally in parts of southern Africa under arid climatic conditions. With $x = 11$ almost certainly basic and fundamental in the tribe Amaryllideae, the *Strumaria-Hessea-Carpolyza* alliance, excluding *H. zeyheri*, seems a natural group with the reduced base number of $x = 10$. The exception which considerably complicates the situation is *H. zeyheri*: the possession of $x = 11$ in this species may represent a contradiction to the assumption that (a) the *Strumaria* alliance is a natural one, and (b) that $x = 10$ is basic in this group.

To answer the first query a survey of the important characteristics of the group is necessary. The name *Strumaria* alludes to the swollen style, which is possessed not only by species of *Strumaria*, but also by some species of *Hessea*. The typical style in Amaryllideae is filiform and the various elaborations possessed by *Strumaria* and some species of *Hessea* seem almost certainly derivative. Those species in the group with filiform styles might then be regarded as primitive. These include *Carpolyza*, as well as *Hessea zeyheri* and its close allies *H. stellaris* and *H. cinnamomea*. Notably, it is only in these few species that the tepals are united in a short tube and the stamens are epipetalous. United tepals and epipetalous stamens occur in most of the Amaryllideae, such as *Crinum, Ammocharis*, many species of *Brunsvigia*, and some species of *Nerine*, and this condition also is probably ancestral within the tribe.

This is morphological evidence supporting the suggestion that *Carpolyza* and the species of *Hessea* with filiform styles and short perianth tubes are primitive in the alliance. If this hypothesis is accepted, the higher base number in *Hessea zeyheri* can be viewed as ancestral, with the base number $x = 11$ being the same as that in the majority of genera of Amaryllideae. Cytological examination of further species of the alliance, especially those related to *H. zeyheri*, may establish some answers to the problem.

A reevaluation of the generic limits may also be called for since certain species of *Hessea* may be more closely related to *Strumaria* in possessing strumose styles, free tepals and stamens, and similar karyotypes. In view of the cytological evidence the traditional distinction between *Hessea* and *Strumaria*, fully outspread tepals and upright flowers as against subpatent tepals in ± pendulous flowers, may be less significant than stylar characteristics and the presence of a perianth tube, as Phillips (1951) infers.

CONCLUSION

Cytological results support the hypothesis that the *Hessea-Strumaria-Carpolyza* alliance comprises a natural group of species related to the tribe Amaryllideae. The group is envisaged as comprising morphologically reduced species specialized for survival in the arid areas of southern Africa. The ancestral chromosome number is probably $x = 11$, found in all Amaryllideae and in *H. zeyheri*; other species of *Hessea* as well as *Carpolyza* and *Strumaria* all have a similar karyotype with $x = 10$ and are presumed to have evolved from a *H. zeyheri*-like ancestor by aneuploid reduction of the base number. The elaborations of the basic filiform style in *Strumaria* and many species of *Hessea* are seen as developments subsequent to the change in basic number. These adaptations set the two genera, which appear in need of redefinition, well apart from *Carpolyza*, which retains many features believed to be primitive in the alliance. *Carpolyza* appears to have followed a different evolutionary pathway from the remainder of the *Hessea-Strumaria* alliance, though probably from a common ancestor with $x = 10$.

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